

Longevity of seed in storage

Model, calculation path and limits

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Abstract

The improved seed viability equation of Ellis and Roberts describes the death of a seed lot as a normally distributed process whose dispersion depends on seed moisture content and storage temperature. From it, half-life, time of regeneration and monitoring interval can be derived. This paper sets out the calculation path, works through an example, and names the three points at which the model is most likely to hold, or not to hold, in genebank practice: at very low temperatures, at very low seed moisture content, and for species for which no documented constants are available.

1. The model

The equation has two parts. The first describes the course over time:

$$v = Ki - p / \sigma$$

Here v is the viability after p days, expressed as a probit, that is, as a normal deviate; Ki the initial viability in the same measure; σ the standard deviation of the death distribution in days. On the probit scale the course is a straight line, on the percentage scale a sigmoid.

The second part describes what σ depends on:

$$\log_{10} \sigma = KE - CW \cdot \log_{10} m - CH \cdot t - CQ \cdot t^2$$

m is the seed moisture content in per cent of fresh weight, t the storage temperature in degrees Celsius. KE , CW , CH and CQ are species-specific constants. KE sets the basic longevity, CW weights the moisture, CH and CQ represent the temperature effect linearly and quadratically. The values usually regarded as universal temperature constants are $CH = 0.0329$ and $CQ = 0.000478$ (Dickie et al. 1990, eight species); across twelve crop species, Ellis and Hong found similar common values (0.0322 and 0.000454), while KE and CW remain species-specific. The data layer holds the Ellis and Hong set as a substitute; the worked example below uses the species-specific barley set. CW tends to be higher in starchy than in oily seeds; Ellis and Hong found values between 4.2 (rice) and 6.0 (maize). Oily seeds bind less water at the same air humidity; when dried to the same relative humidity they reach a lower moisture content by themselves.

2. The calculation path

The path from question to answer has four steps.

Step 1 — initial value as a probit. An initial germination of 95 per cent corresponds to a normal deviate of 1.645.

Step 2 — calculate σ . For barley ($KE = 9.983$; $CW = 5.896$; $CH = 0.040$; $CQ = 0.000428$) at 5 per cent seed moisture content and minus 18 degrees:

$$\begin{aligned}\log_{10} \sigma &= 9.983 - 5.896 \cdot \log_{10}(5) - 0.040 \cdot (-18) - 0.000428 \cdot 324 \\ &= 9.983 - 4.121 + 0.720 - 0.139 \\ &= 6.443 \\ \sigma &= 10^{6.443} \approx 2.77 \cdot 10^6 \text{ days} \approx 7596 \text{ years}\end{aligned}$$

Step 3 — insert the target value. The regeneration threshold of the FAO standards lies at 85 per cent of the initial value, here therefore at 80.75 per cent germination, corresponding to a normal deviate of 0.869. The time to reach it:

$$p = (1.645 - 0.869) \cdot \sigma \approx 0.776 \cdot 7596 \text{ years} \approx 5896 \text{ years}$$

Step 4 — monitoring interval. The standards set the monitoring interval at one third of this time or less, but no longer than 40 years (standard 4.3.3). The calculated third of around 1965 years is therefore replaced by the upper limit of 40 years. The standards also provide fallback intervals of ten years for species expected to be long-lived and five years or less for those expected to be short-lived; these apply only where no prediction can be made and accessions are held at -18°C in hermetically closed containers.

Even 40 years should not be read as a testing schedule without further thought. The calculated value lies far outside the range in which the model has been validated experimentally (section 4), and the model tends to overestimate longevity in the sub-zero range. This strand therefore recommends scheduling the first retest no later than after ten years and setting the interval thereafter from the measured values. This is a precautionary rule of this strand, not a requirement of the standards.

3. Figures for orders of magnitude

The following table gives, for barley at 95 per cent initial germination, the time to the regeneration threshold in years. It shows how strongly the two control variables act.

Seed moisture content	20 °C	10 °C	5 °C	0 °C	-18 °C
12 %	0.9	3.2	5.5	8.9	33.8
10 %	2.8	9.4	16.0	26.0	99.0
8 %	10.3	34.9	59.6	96.8	369
6 %	56.4	190	325	528	2012
5 %	165	558	952	1546	5896
4 %	616	2079	3547	5762	21,975

Two readings are essential. First, moisture acts more strongly than temperature: going from 12 to 4 per cent seed moisture content gains a factor of 600 to 700 at the same temperature, going from 20 to minus 18 degrees a factor of 35 at the same moisture. Second, the values in the lower left corner are so large that they cannot be taken seriously as a prediction — and that is precisely what the next section addresses.

4. The three limits

4.1 The temperature limit

The experimentally verified range of the equation extends from minus 13 to 90 degrees Celsius. The standard condition of the base collection, minus 18 degrees, lies below it. Every calculation for standard storage is therefore an extrapolation beyond the verified range. Long-term trials in genebanks indicate that longevity tends to be overestimated in this range (section 4.2). The tool of the package flags this circumstance for every calculation in the freezing range.

4.2 Overestimation in the freezing range

Walters, Wheeler and Stanwood (2004) found a break in the Arrhenius plot at about -15°C . Below it, ageing proceeded faster than extrapolation from higher temperatures would suggest ("faster deterioration than anticipated from extrapolation of kinetics measured at higher temperatures"). In addition, the benefit of storage at -18°C was progressively lost if the seed had first been stored at 5°C .

Walters, Wheeler and Grotenhuis (2005) analysed about 42,000 accessions of 276 species in the United States National Plant Germplasm System (NPGS), harvested between 1934 and 1975. Viability decreased at both 5°C and -18°C , and did so at variable rates. Short-lived families included, for example, Apiaceae and Brassicaceae; long-lived families included Malvaceae and Chenopodiaceae.

Solberg et al. (2020) summarise the findings in a systematic review. The median P50, the time to a decline to 50 per cent germination, was 42 years in the dataset of Walters et al. (2005) — the seed there was stored at $+5^{\circ}\text{C}$ until 1977 and at -18°C thereafter — and 47 and 56 years in two other studies. Predictions from the Seed Information Database were three to ten times, in some cases more than 40 times, higher than the observed values. This comparison should be read with caution: in these comparisons the predictions were calculated for $+5^{\circ}\text{C}$, and the authors attribute the gap partly to the handling of seed in genebanks.

There is also counter-evidence. At the Dutch genebank CGN, according to van Treuren, de Groot and van Hintum (2013), of nearly 40,000 germination tests after up to 25 years of storage at -20°C (3 to 7 per cent seed moisture content, foil bags), only 3.3 per cent of the monitoring tests fell below the threshold. Li and Pritchard (2009), by contrast, see "relatively widespread evidence of less than expected longevity at conventional seed bank temperatures" and use it to argue for storage at very low temperatures.

For the calculation this means: values of the equation below about -15°C are to be read as an upper estimate, not as an expected value. Monitoring of germination remains mandatory in every case.

4.3 The moisture limit

Below a seed moisture content of about 2 to 6 per cent, further drying brings no further gain in longevity. The equation does not know this lower bound: it continues to calculate and delivers values for 2 per cent moisture that are not physically supported. Anyone extrapolating the table above to the left leaves the model.

4.4 The species limit

Documented sets of constants exist for a manageable number of species. For the great majority of the accessions of a genebank, and all the more for wild species, none are available. Three ways out are customary, and all three are to be used with reservation:

- transfer from a related species with a similar oil content,
- use of the common temperature constants of Ellis and Hong with estimated **KE** and **CW**,

- own derivation via accelerated ageing, which requires an experimental set-up and time.

The tool accepts freely entered sets of constants and marks the result as unverified. External constants without a source reference are not taken into the data layer of the strand.

The data layer holds the following documented sets. The essential point is that **KE** and **CW** must always be used together with the **CH** and **CQ** values with which they were fitted. Sets of different origin must not be mixed.

Species	KE	CW	CH	CQ	Source	Status
Barley (<i>Hordeum vulgare</i>)	9.983	5.896	0.040	0.000428	Ellis and Roberts 1980	verified
Flooded gum (<i>Eucalyptus grandis</i>)	9.661	6.467	0.03498	0.000233	Fantinatti and Usberti 2007	verified
Chickpea (<i>Cicer arietinum</i>)	8.901	4.847	0.0329	0.000478	Dickie et al. 1990, Table 1	verified
Soybean (<i>Glycine max</i>)	7.525	4.086	0.0329	0.000478	Dickie et al. 1990, Table 1	verified
Cowpea (<i>Vigna unguiculata</i>)	9.401	5.118	0.0329	0.000478	Dickie et al. 1990, Table 1	verified
Lettuce (<i>Lactuca sativa</i>)	8.218	4.797	0.0489	0.000365	Kraak and Vos 1987	verified
Pea (<i>Pisum sativum</i>)	9.858	5.390	0.0329	0.000478	Ellis, Hong and Roberts 1989, via Pritchard and Dickie 2003	partially verified
Groundnut (<i>Arachis hypogaea</i>)	6.177	3.426	0.0304	0.000453	Usberti and Gomes 1998	verified
Common temperature set	–	–	0.0322	0.000454	Ellis and Hong 2007	partially verified

Chickpea, soybean and cowpea were fitted by Dickie et al. (1990, Table 1) with the common temperature constants **CH** = 0.0329 and **CQ** = 0.000478; the data range extends from –13 to 90 °C and from 1.8 to 25 per cent seed moisture content. The lettuce set of Kraak and Vos (1987) has its own temperature constants and is valid for 5 to 75 °C and 3.6 to 13.6 per cent seed moisture content; at –20 °C, freezing damage occurs above about 12 per cent seed moisture content. Dickie et al. (1990) give **KE** = 6.985 and **CW** = 4.200 for lettuce with the common temperature constants; this set cannot be mixed with that of Kraak and Vos. The pea set of Ellis, Hong and Roberts (1989), as reproduced by Pritchard and Dickie (2003), rests on a trial at a single temperature (65 °C) and is therefore only partially verified. The groundnut set of Usberti and Gomes (1998) has its own temperature constants.

The species-specific sets of Ellis and Hong (2007) for wheat, rice, maize and sorghum were available only in a secondary compilation and were not adopted.

5. Relation to the genebank standards

The FAO standards translate the model into operational requirements:

Requirement	Value
Base collection	–18 ± 3 °C, 15 ± 3 % relative humidity, hermetically sealed
Active collection	5 to 10 °C, 15 ± 3 % relative humidity

Requirement	Value
Drying before storage	5 to 20 °C at 10 to 25 % relative humidity
Initial germination	above 85 % for most crop species
Monitoring interval	one third of the time to 85 % of the initial value or less, no longer than 40 years (4.3.3)
Fallback interval, only without prediction and at -18 °C hermetic	10 years long-lived, at most 5 years short-lived
Regeneration	below 85 % of the initial value or remaining quantity below the requirement for three sowings
Minimum quantity	around 1500 seeds for self-pollinating, 3000 for cross-pollinating species

Noteworthy is the linking of regeneration to two conditions: germination **or** remaining quantity. In practice the second condition is often the binding one. A frequently requested accession must be propagated long before it has an ageing problem.

Figures

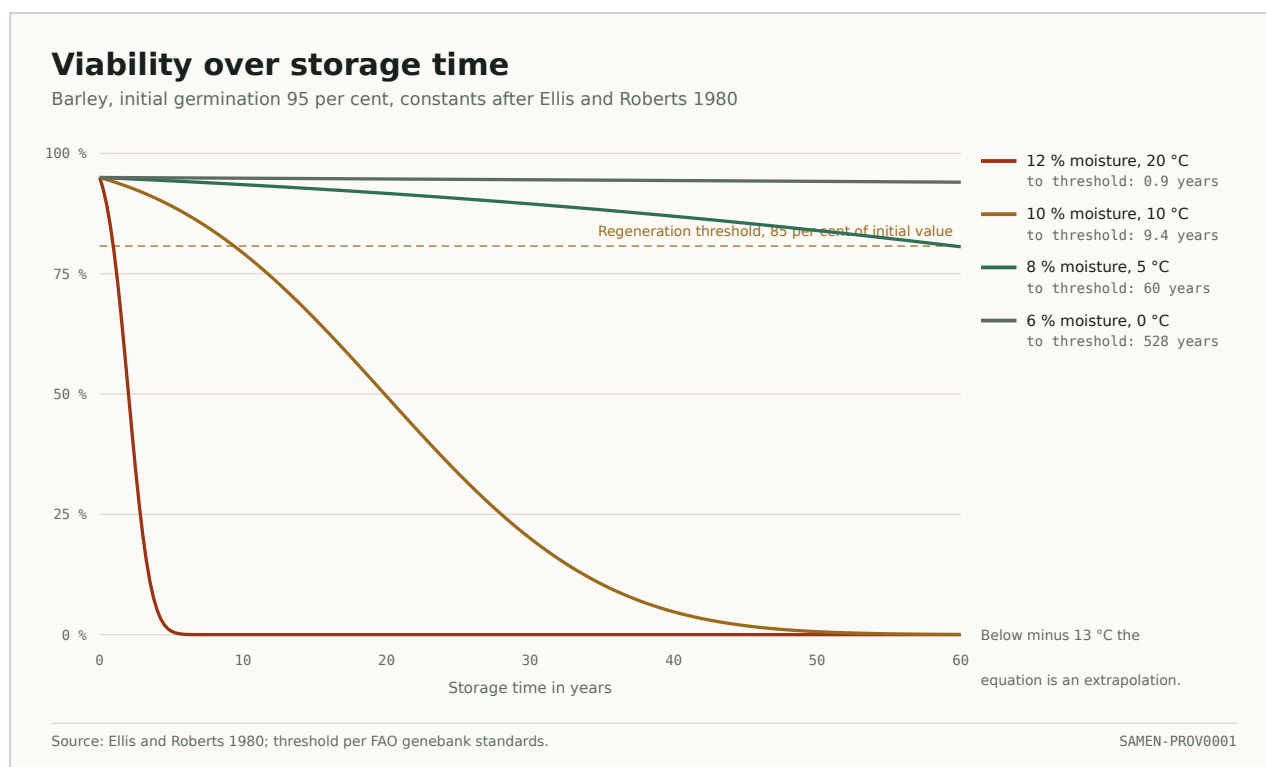


Figure 1. Viability of barley over time. Source: data layer of the strand, see figure footer.

Limits of this paper

The paper deals with orthodox seed. Recalcitrant and intermediate species follow other regularities and are not covered here. The sets of constants in the data layer cover eight documented species and one common set for the temperature terms (section 4.4); further sets scattered through the literature, including the Ellis and Hong (2007) sets for wheat, rice, maize and sorghum, were deliberately not adopted unverified. Overestimation in the freezing range is set out in section 4.2 on the basis of the literature; no quantification of our own based on genebank data has been carried out.

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